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EARLY MIOCENE ANURANS FROM FLORIDA

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The early Miocene beds of the Thomas Farm of Gilchrist County, Florida, have produced the most diverse anuran fauna known from the Tertiary of North America. Indeed, all six anuran families indigenous to Florida today are represented in these Miocene sediments. Previous references to Thomas Farm frogs and toads have been summarized by Holman (1961). A comprehensive list of the Thomas Farm vertebrates with references is found in Olsen (1962). Since Olsen's paper, Auffenberg (1963) has discussed snake material, and Estes (1963) has reported on salamander and lizard fossils. Several of these authors have discussed the stratigraphy of the deposit.

Large numbers of additional anuran bones have recently accumulated through the intensive collecting of workers affiliated with the Florida Geological Survey and the University of Florida. These new bones have been submitted to me for identification, and the present report deals with the leptodactylid, ranid, and brevicipitid frogs of the deposit. A second report on the bufonid, hylid, and pelobatid frogs is anticipated as soon as enough recent skeletons of these groups become available.

Materials and Methods

I have previously found the ilium to be a reliable element in the identification of fossil anuran remains (Holman, 1959, 1961, 1962a, 1962b, 1963a, 1963b). Other workers have also found the ilium to be useful (see Auffenberg, 1956, 1957, 1958; Lynch, 1964; Tihen, 1962; and especially Chantell, 1964). I now regard the ilium as the best single element upon which to base the identification and description of fossil frogs, and I suggest that this element be designated as the type specimen when descriptions based on disarticulated anuran material are made. The sacrum, which Taylor (1942) favors, is quite subject to individual variation. In fact, it may show individual variation in characters that are considered to be definitive at the subordinal level (Holman, 1963c). Nevertheless, the sacrum is a good postcranial element for the substantiation of ilial identifications. Other postcranial elements are untrustworthy, and unfortunately, fossil anuran cranial elements

are usually in the form of tiny fragments of disarticulated skull bones.

Anuran skeletons at Illinois State University and material borrowed or received as gifts from individuals in the acknowledgments section have been utilized as comparative material. The following abbreviations are used: M.C.Z.—Museum of Comparative Zoology; U.F.—University of Florida; F.G.S.—Florida Geological Survey. All measurements are in millimeters.

ACKNOWLEDGMENTS

I wish to thank Bryan Patterson, Stanley J. Olsen, and Clayton Ray for the privilege of studying the fossil material in their care. Several persons have generously loaned or given comparative material used in this study. These people include: W. Auffenberg and P. Brodkorb, Gainesville, Florida; J. D. Lynch and H. M. Smith, Urbana, Illinois; W. F. Blair, Austin, Texas; R. S. Simmons, Baltimore, Maryland; G. B. Rabb, Brookfield, Illinois; and J. A. Peters and W. J. Riemer, Washington, D. C. Donna Rae Holman made the drawings.

FAMILY LEPTODACTYLIDAE

Heretofore, the only pre-Pleistocene record of the Leptodactylidae from North America is that of Estes (1964), who assigned a right squamosal to "Family incertae sedis, near Leptodactylidae?". *Eleutherodactylus augusti* and *Syrrhophis marnocki* have been reported from the Pleistocene of Texas (Mecham, 1959; Tihen, 1960; Lynch, 1964).

Genus *Leptodactylus* Fitzinger

In the study of leptodactylid fossils the following recent skeletons were examined: *Ceratophrys cornuta* 1, *C. varia* 1, *Eleutherodactylus augusti* 1, *E. dunni* 5, *E. podociferus* 2, *E. ricordi* 2, *Eupemphix pustulosa* 4, *Leptodactylus insularum* 3, *L. melanonotus* 5, *Miobatrachus gouldi* 1, *Tomodactylus nitidus* 2, and *Syrrhophus marnocki* 1.

In concordance with the great adaptive radiation of the Leptodactylidae their ilia show many striking intergeneric differences. The ilial crest is absent in *Ceratophrys, Eupemphix,* and *Miobatrachus.* The other genera show an interesting convergence with some genera of the Ranidae in that an ilial crest is present. In

Eleutherodactylus dunni the crest is high throughout, but it is extremely thin and has a membranous appearance. In *E. augusti, E. podociferus, E. ricordi,* and *Leptodactylus* the crest is moderately high and is thin with the exception of *E. augusti,* which has a somewhat thicker crest. In *Syrrhophus* and *Tomodactylus* the crest is obsolete. There is great variability in the prominence for the origin of the vastus externus head of the M. triceps femoris (for the sake of brevity this structure will hereafter be referred to as the vastus prominence). In *Ceratophrys* it is a much produced dorsal spike, whereas in *Miobatrachus* it is obsolete. In *Eleutherodactylus, Eupemphix, Syrrhophus,* and *Tomodactylus* it is small to medium in size, ovaloid to round in shape, and moderately to strongly swollen. In *Leptodactylus* it is larger and is usually strongly beveled.

Thus, the ilia of *Leptodactylus* may be distinguished from other Leptodactylidae at hand by the following combination of characters: ilium with crest present, moderately high, thin; vastus prominence large, usually strongly beveled.

Figure 1 shows the distribution of muscular origins on an ilium of *Leptodactylus melanonotus.* The muscles of two *Leptodactylus insularum* specimens were also studied. Whenever possible I have tried to use terminology consistent with ilial musculature. Five ilia from the Thomas Farm represent a new species of *Leptodactylus,* the first fossil leptodactylid described from North America.

Leptodactylus abavus sp. nov.

Holotype. Right ilium, U.F. 10201 (Fig. 1). From Hawthorne formation, lower Miocene, Arikareean; Thomas Farm, Gilchrist County, Florida. Collected by Clayton Ray.

Paratypes. Right ilium, F.G.S. V-6067; two right and one left ilia, U.F. 10202, from the same locality as the holotype.

Referred elements. Two sacra, F.G.S. V-6068 and M.C.Z. 3406.

Diagnosis. A small Miocene *Leptodactylus* showing similarities to recent *L. melanonotus,* but differing in having; posterodorsal border of ilium sloping gently into dorsal acetabular expansion (*L. melanonotus* with this border sloping more abruptly into dorsal acetabular expansion); vastus prominence more produced and extensive, with valley between it and dorsal acetabular border deeper; angle between ventral acetabular expansion and shaft greater

than 90 degrees (*L. melanonotus* with angle less than 90 degrees). Measurements: greatest height through acetabulum 2.3; greatest height through ilial crest 2.2; greatest length of vastus prominence 2.4 mm.

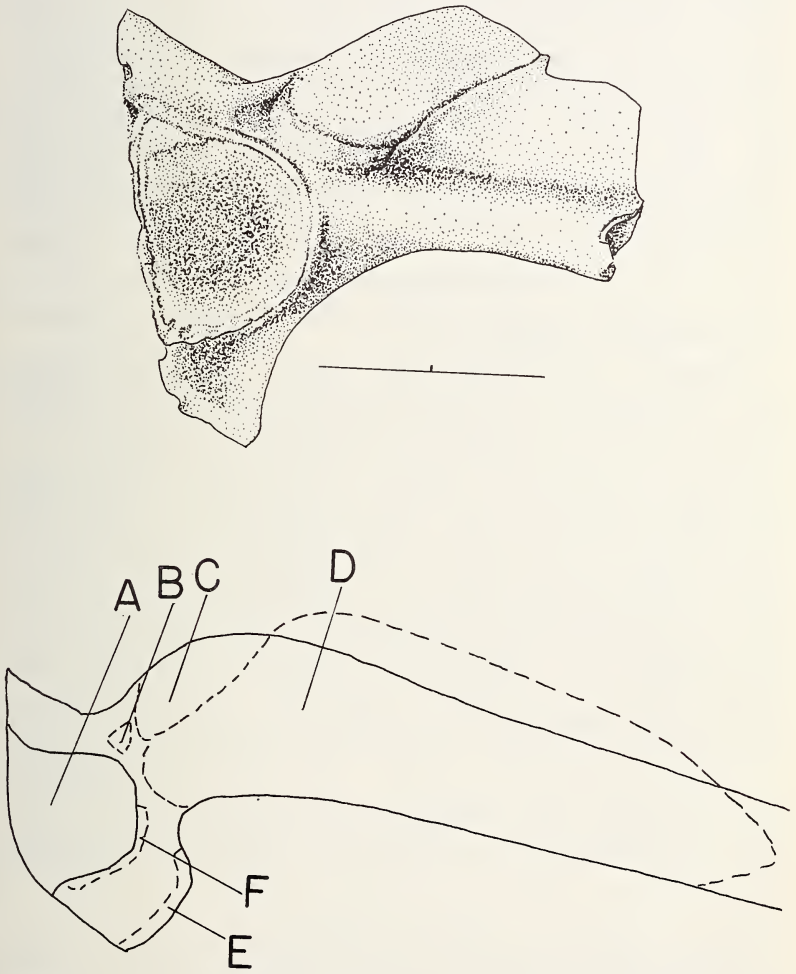

Fig. 1. Top, holotype right ilium of *Leptodactylus abavus* sp. nov., U.F. 10201 (line represents 2 mm.). Bottom, ilium drawn from *Leptodactylus melanonotus* to illustrate origin of selected muscles: A, acetabular fossa; B, tendinous origin of M. biceps femoris; C, fleshy origin of vastus externus head of M. triceps femoris; D, fleshy origin of M. gluteus; E, tendinous origin of M. sartorius; F, tendinous origin of vastus internus head of M. triceps femoris.

Etymology. Latin, *abavus,* masculine, a grandfather's grandfather, an ancestor.

Description of holotype. The dorsal acetabular expansion is complete, moderate in size, and acute dorsally. The pit for the tendinous origin of the M. biceps femoris is small, round, and shallow. The posterodorsal border of the ilial crest slopes gently into the base of the dorsal acetabular expansion. The vastus prominence is much enlarged, rhomboidal in shape, strongly beveled, and lacks bordering ridges. The ilial crest is moderately developed, quite thin, and its lateral surface is strongly excavated. Much of the anterior portion of the ilium is missing. The angle between the shaft and the base of the ventral acetabular expansion is greater than 90 degrees. Only a small part of the posterior border of the ventral acetabular expansion is broken. This expansion is small and acute ventrally. The acetabulum is large and broadly rounded anteriorly.

Paratypes. There is very little variation among the paratype ilia. One ilium has the vastus prominence not quite as strongly beveled, but this is probably due to individual variation.

Sacra. Two sacra representing small leptodactylid frogs differ somewhat from the sacra of recent *L. melanonotus.* In the fossils the cylindrical shape of the sacral diapophyses is evident even though their tips are broken. The prezygapophyseal faces are pointed (somewhat less pointed in *L. melanonotus*) and have their long axes almost parallel to the long axis of the centrum (long axes more oblique in *L. melanonotus*). A strong thin ridge runs transversely across the top of the neural arch. The neural canal is much broader than high. The condyles lie very close to one another (slightly separated in *L. melanonotus*). The centra are broader than long through the condyles. The cotyla of both fossils are depressed. The width through the condyles of the F.G.S. specimen is 1.6, whereas this width is 1.3 mm in the M.C.Z. specimen.

Family Ranidae

All New World fossils of the family Ranidae have been assigned to the genus *Rana.* Tihen (1951) and Auffenberg (1956) list *Rana* sp. from the lower Miocene of the Thomas Farm of Florida. *Rana johnsoni* La Rivers from the lower Pliocene of Storey County, Nevada (La Rivers, 1953), and *Rana pliocenica* Zweifel from the

middle Pliocene of Contra Costa County, California (Zweifel, 1954), are heretofore the earliest named species of New World *Rana*. Nine *Rana* species have been described from the upper Pliocene of Meade County, Kansas (see Taylor, 1942, and Holman, 1963b). These species should be considered *species inquirendae* until the Kansas bones have been re-studied.

Pleistocene ranids definitely assigned to species are all represented by forms living today. These fossils include: *Rana catesbeiana* (Sangamon, Meade County, Kansas, Tihen, 1954); *Rana grylio* (Illinoian?, Alachua County, Florida, Tihen, 1952), and *Rana pipiens* (various localities in Florida, Holman, 1962a; Kansas, Tihen, 1954; and Texas, Holman, 1962b and 1964, and Mecham, 1959).

Genus *Rana* Linnaeus

The ilia of recent New World *Rana* studied (*R. areolata* 3, *R. aurora* 1, *R. boylii* 2, *R. capito* 1, *R. cascadae* 1, *R. catesbeiana* 17, *R. clamitans* 8, *R. grylio* 3, *R. heckscheri* 3, *R. palmipes* 3, *R. palustris* 1, *R. pipiens* 77, *R. sylvatica* 5) and of *R. esculenta* (1) of the Old World are distinct from 2 *R. temporaria* and a small assemblage of other ranid genera available. In the former group the ilial crest is well developed and the vastus prominence is flattened laterally and is not produced above the level of the ilial crest anterially. In *Rana temporaria* and 1 *Ooeidozyga laevis* the ilial crest is less developed, and the vastus prominence is flattened, but is moderately (*R. temporaria*) or much (*O. laevis*) produced above the level of the ilial crest anteriorly. In 1 *Cacosternum boettzeni*, 2 *Mantella auriantiaca*, 1 *Rhacophorus buergeri*, and 3 *Staurois natator* the ilial crest is absent, and the vastus prominence is knob-like.

New World species of *Rana* (including *R. esculenta*) separate into two groups based on ilial characters. In *R. areolata*, *R. capito*, *R. cascadae*, *R. palmipes*, *R. palustris*, *R. pipiens*, and *R. sylvatica* the posterodorsal border of the ilial crest slopes gently into the dorsal acetabular expansion. In *R. aurora*, *R. boyli*, *R. catesbeiana*, *R. clamitans*, *R. esculenta*, *R. grylio*, and *R. heckscheri* the posterodorsal border of the ilial crest slopes precipitously into the dorsal acetabular expansion. This condition was first noticed by Auffenberg (1956) who used different terminology to describe it. Whether the condition indicates natural groupings is unknown at

present. The ilia of Thomas Farm ranid frogs represent the genus *Rana,* being similar to the former assemblage of *Rana* species in this character.

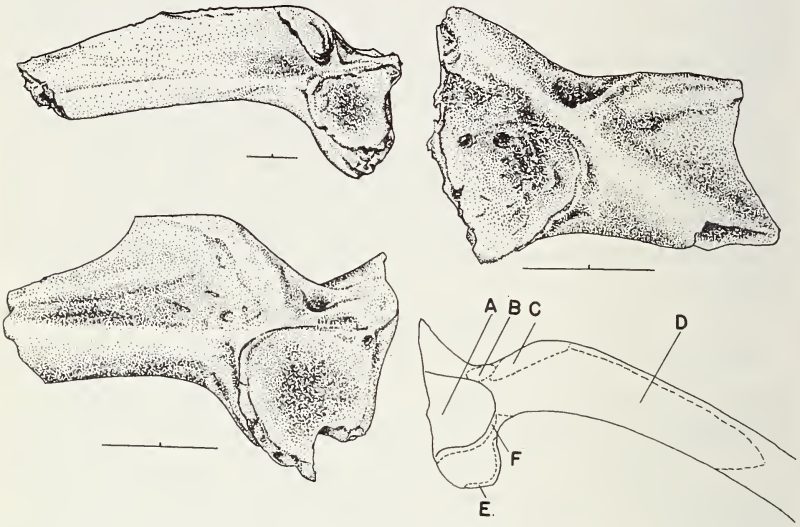

Fig. 2. Top left, holotype left ilium of *Rana miocenica* sp. nov., F.G.S. V-6069; top right, holotype right ilium of *Rana bucella* sp. nov., F.G.S. V-6071; bottom left, left ilium of *Rana* cf. *R. pipiens,* U.F. 10203 (each line represents 2 mm). Bottom right, ilium drawn from *Rana pipiens* to illustrate origin of selected muscles: A, acetabular fossa; B, tendinous origin of M. biceps femoris; C, fleshy origin of vastus externus head of M. triceps femoris; D, fleshy origin of M. gluteus; E, tendinous origin of M. sartorius; F, tendinous origin of vastus internus head of M. triceps femoris.

Figure 2 shows the distribution of muscular origins on an ilium of *Rana pipiens. Rana catesbeiana* specimens were also dissected. I have attempted to use terminology consistent with the musculature of the *Rana* ilium whenever possible.

Two new species of *Rana* from the lower Miocene of the Thomas Farm of Florida are detailed in the following paragraphs. These fossil frogs represent the earliest ranids described from North America.

Rana miocenica sp. nov.

Holotype. Left ilium F.G.S. V-6069 (Fig. 2). From Hawthorne formation, lower Miocene, Arikareean; Thomas Farm, Gilchrist County, Florida. Collected by Pierce Brodkorb, November 14, 1959.

Referred element. Sacral vertebra F.G.S. V-6070. Collected from the same locality by the same collector in 1962.

Diagnosis. A medium-sized Miocene *Rana* similar to *R. areolata, R. capito, R. cascadae, R. palmipes, R. palustris, R. pipiens,* and *R. sylvatica* in having posterodorsal border of ilial crest sloping gently into dorsal acetabular expansion, but differing in having vastus prominence relatively short, but much produced, and with strong bordering ridges (other species with this prominence usually more elongate, less produced; if bordering ridges present, never as extensive or strong); also differing from the above species (*R. palmipes* being a single exception) in having posteorodorsal border of ilial crest along medial attachment of dorsal fascia swollen (other species with this border blade-like). Measurements: greatest height of acetabular fossa 3.3; highest part of ilial shaft 4.0; greatest length of vastus prominence 3.1 mm.

Description of holotype. Much of the dorsal acetabular expansion is broken. The pit for the tendinous origin of the M. biceps femoris is moderately large and is triangular in shape. The posterodorsal border of the ilial crest slopes gently into the dorsal acetabular expansion. The vastus prominence is relatively short, but much produced and has strong bordering ridges. It is ovaloid in shape and flattened laterally. The ilial crest is well developed and high, and its lateral surface is moderately excavated. Part of the anterior portion of the ilium is broken. The angle between the shaft and the ventral acetabular expansion is greater than 90 degrees. Much of the ventral acetabular expansion is broken. The acetabulum is moderate in size, about as long as high, and is moderately excavated. The anterior border of the acetabulum appears to be narrowly rounded, although some of the acetabular border is chipped. The posterodorsal border of the ilial crest along the medial attachment of the dorsal fascia is swollen.

Sacrum. The referred sacrum originates from an individual of about the same size as the one represented by the holotype. The fossil vertebra is a typical *Rana* sacrum with one anteriorly directed condyle and two posteriorly directed condyles. The diapophyses are cylindrical. The left diapophysis has a single anterior tubercle at about the middle of its extent, and the right diapophysis has a divided anterior tubercle at about the middle of its extent. The prezygapophyseal faces are ovaloid in shape, and just behind them, on the top of the neural arch, is a flattened tri-

angular area. The neural canal is about twice as wide as high. The posterior condyles are depressed and separated from each other by a space a little less than half the width of one condyle. The centrum is as broad as it is long through the condyles. The anterior condyle is much depressed. The width of the sacrum through the diapophyses is 10.0; the width of the centrum through the condyles is 3.2; the length of the sacrum through the condyles is 3.2 mm.

The fact that the length of the centrum divided by the width of the centrum is 1.0 is interesting in that it places the fossil closer to *R. pipiens* rather than to *R. catesbeiana, R. grylio,* and *R. heckscheri* based on the data of Tihen (1954, p. 219, fig. 1).

Remarks. Rana miocenica was a frog about the size of a recent *Rana pipiens* with a snout-vent length of about 90 mm. The relationships of *R. miocenica* to an assemblage of recent *Rana* with the gently sloping posterodorsal border of the ilium is apparent, but it is difficult to ally the fossil to any one of these species because of their great similarity to each other. Nevertheless, *R. miocenica* shows some similarity to three recent skeletones of *R. palmipes* in the development of the knob-like condition of the posterodorsal border of the ilial blade along the medial attachment of the dorsal fascia. In *R. palmipes* the condition is not as pronounced as in the fossil. Also, in the three recent skeletons of *R. palmipes* the sacrum is fused to the vertebra that proceeds it. The sacrum assigned to *R. miocenica* is free.

An assemblage of ilia from the upper Pliocene of Meade County, Kansas are figured by Taylor (1942). Most of these are assigned to the genus *Rana,* but none are identified to species. These ilia have the vastus prominence elongate and without strong bordering ridges, thus differing from *R. miocenica. Rana pliocenica* Zweifel from the middle Pliocene of Contra Costa County, California, differs from *R. miocenica* in that the posterodorsal border of the ilial crest slopes precipitously into the dorsal acetabular expansion (Zweifel, 1954, p. 85, fig. 1).

Rana bucella sp. nov.

Holotype. Right ilium F.G.S. V-6071 (Fig. 2). From Hawthorne formation, lower Miocene, Arikareean; Thomas Farm, Gilchrist County, Florida. Collected by Pierce Brodkorb, June, 1958.

Diagnosis. A small Miocene *Rana* showing no close affinities to recent or fossil *Rana* species studied, and differing strikingly from all of these in having a very slight slope between the posterodorsal border of the ilial crest and the dorsal acetabular expansion, and in having the pit for the tendinous origin of the M. biceps femoris much enlarged. Measurements: greatest height of ilial shaft 2.7; greatest length of biceps femoris pit 1.3 mm.

Etymology. Latin, *bucella,* feminine, diminutive of *buccea,* feminine, a morsal, a mouthful, in reference to the diminutive size of the fossil species.

Description of holotype. The tip of the dorsal acetabular expansion is broken. The biceps femoris pit is much enlarged and is triangular in shape. The posterodorsal border of the ilial crest has a very slight slope into the dorsal acetabular expansion. The vastus prominence is relatively elongate, not highly produced, lacks bordering ridges, and is ovaloid in shape. The ilial crest is well developed and its lateral surface is rather deeply excavated. Much of the anterior portion of the ilium is broken. The angle between the ilial shaft and the ventral acetabular expansion is impossible to measure because so much of the ventral acetabular expansion is broken. The acetabulum is moderate in size, higher than long, and is rather shallowly excavated. The anterior border of the acetabulum is narrowly rounded. The posterodorsal border of the ilial crest along the medial attachment of the dorsal fascia is bladelike.

Remarks. Rana miocenica shows certain resemblances to living North American species of *Rana,* especially in the conformation of the posterior part of the ilium, but *Rana bucella* is quite different from all living and fossil *Rana* studied. A new generic name might be in order if it were not for the fact that other genera of the Ranidae such as *Staurois* and *Ooeidozyga* depart even more from the ilial structure of *Rana.* It is here suggested that *R. bucella* has no close relatives among living species of the genus. *Rana bucella* lacks the numerous small perforations of the ilium that are characteristic of newly metamorphosed and young ranids, thus the fossil represents an adult or subadult.

Rana cf. *Rana pipiens*

Material. Left ilium, U.F. 10203 (Fig. 2), right ilium, M.C.Z. 1994.

Remarks. These ilia are indistinguishable from a large series of recent *R. pipiens,* and although other recent species of *Rana* are very similar to *R. pipiens* it seems wise to suggest that the closest relationships of the fossils are with this species based on present geographic distributions.

M.C.Z. 1994 has already been listed as *Rana* sp. by Tihen (1951). It is a small fragmentary bone, but it has the posterodorsal border of the ilium sloping gently into the dorsal acetabular expansion, and the vastus prominence indistinct and lacking bordering ridges. This condition is often seen in young specimens of *R. pipiens* with ilia of about the same size as M.C.Z. 1994.

Two other fragmentary ilia that I have been unable to locate (U.F. 5919) were discussed by Auffenberg (1956). He suggests these ilia are similar to those in an assemblage of frogs that includes *R. pipiens.*

U.F. 10203 appears to be the most complete of the four ilia that are similar to recent *R. pipiens.* A description of this bone is as follows. The tip of the dorsal acetabular expansion is broken. The pit for the origin of the M. biceps femoris is moderately large and is subtriangular in shape. The posterodorsal border of the ilial crest slopes gently into the dorsal acetabular expansion. The vastus prominence is relatively elongate, but rather indistinct, and it lacks bordering ridges. It is ovaloid in shape. The ilial crest is well developed and high throughout and has its lateral surface well excavated, especially along its dorsal portion. The anterior portion of the ilium is broken. The angle between the shaft and the ventral acetabular expansion is greater than 90 degrees. The ventral acetabular expansion is broken except for its base. The acetabulum is moderate in size, about as high as long, and is moderately excavated. The anterior border of the acetabulum is broadly rounded. The posterodorsal border of the ilial crest along the medial attachment of the dorsal fascia is blade-like. Measurements: greatest height of ilial shaft 2.9; greatest length of vastus prominence 2.3; greatest height of acetabulum 2.7 mm.

Rana sp. indet.

The following elements are assigned to the genus *Rana,* but specific allocations are not suggested: scapulae, 3 (U.F. 10204 and 6580, M.C.Z. 3407); humeri, 7 (U.F. 10205 and 6580, M.C.Z. 2003, F.G.S. V-6072); radio-ulnae, 1 (U.F. 10206); tibiofibulae, 2 (M.C.Z. 2001).

FAMILY BREVICIPITIDAE

The only brevicipitid frog genus reported thus far from the North American fossil record is *Gastrophryne*. Auffenberg (1956) has listed *Gastrophryne* from the lower Miocene of the Thomas Farm of Florida; *Gastrophryne carolinensis* has been reported from the Pleistocene of Florida (Holman, 1962a); and *Gastrophryne olivacea* has been reported from the Pleistocene of Texas (Holman, 1963a).

Genus *Gastrophryne* Fitzinger

I have re-examined the specimen (U.F. 5144) that Auffenberg referred to the genus *Gastrophryne*, and I am in full accordance with his generic designation. The dorsal prominence of 2 *Hypopachus cuneus*, and 1 *H. oxyrhinus* is larger and more produced from the shaft than that of *Gastrophryne* (see Holman, 1963a, p. 156, fig. 1 for illustrations of the ilia of *Hypopachus* and *Gastrophryne*). The fossil agrees with *Gastrophryne* in this character. Additional brevicipitid comparative material has become available that indicates the fossil is indistinguishable from recent 6 *G. carolinensis*, but is quite different from 3 *G. olivacea*. Therefore, I wish to tentatively refer the Thomas Farm ilium to the former species.

Gastrophryne cf. *Gastrophryne carolinensis*

Material. Right ilium, U.F. 5144. See Auffenberg (1956, p. 7) for a figure of this specimen.

Remarks. There are striking differences between the ilia of *G. carolinensis* and *G. olivacea* that have been discussed by Holman (1963a, p. 155), who figures the ilia of these two species (p. 156, fig. b and c). Although part of the ventral acetabular expansion of the fossil is broken (not as much as is shown in Auffenberg's figure) the fossil clearly shows its relationships are with *G. carolinensis*.

DISCUSSION AND SUMMARY

The three anuran families (Leptodactylidae, Ranidae, and Brevicipitidae) detailed in this paper are all indigenous to Florida today. All of the three genera reported (*Leptodactylus*, *Rana*, and *Gastrophryne*) are extant, and with the exception of *Leptodactylus* are present in modern Florida. Of the five species dis-

cussed (*L. abavus, R. miocenica, R. bucella, R.* cf. *R. pipiens,* and *G.* cf. *G. carolinensis*), the first three are extinct, and the last two have been tentatively referred to species living in Florida today.

Only one species of Leptodactylidae occurs in Florida today, and this form, *Eleutherodactylus ricordi,* has been introduced from the West Indies (Carr and Goin, 1955). *Leptodactylus* presently ranges from southern Texas and Sonora to Argentina, the Antilles, and the islands of San Andres and Providence (Smith and Taylor, 1948).

Six species of *Rana* occur in Florida today (Carr and Goin, 1955). Three of these are large bullfrogs (*R. catesbeiana, R. heckscheri,* and *R. grylio*), two are moderately large (*R. capito* and *R. clamitans*), and one (*R. pipiens*) is a medium-sized frog. It is interesting to note that two of the fossil species (*R. miocenica* and *R.* cf. *R. pipiens*) are medium-sized frogs, whereas the third (*R. bucella*) is a diminutive *Rana.* The absence of large bullfrogs from the early Miocene of the Thomas Farm is unexplainable at present.

The only brevicipitid present from the Thomas Farm shows its relationships with recent *Gastrophryne carolinensis,* a frog that ranges through southeastern United States today, rather than with the southwestern forms *G. olivacea* and *Hypopachus.*

A more detailed discussion of the affinities of the fossil anuran fauna, and remarks on the paleoenvironment of the Thomas Farm are deferred until the remaining fossil anuran families are studied.

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